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Fish community and abundance response to improved connectivity and more natural hydromorphology in a post-industrial subcatchment

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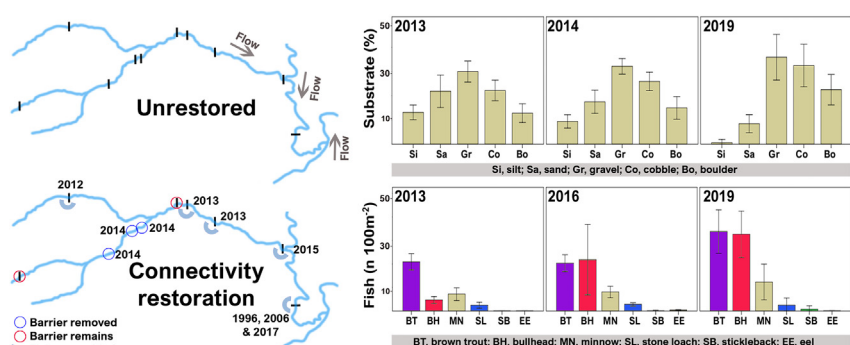
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HIGHLIGHTS

- Subcatchment connectivity restoration benefitted most native stream fish species.
- After connectivity restoration, riffle habitat increased and fine sediment reduced.
- Post-restoration, abundance of sensitive rheophilic fish took 3 years to increase.
- Mean age of brown trout decreased, reflecting an increased migratory component.
- Native stream fishes benefitted more from barrier removal than fishway provision.

GRAPHICAL ABSTRACT



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ABSTRACT

Barrier removal and fish pass construction are increasingly used as tools to restore river connectivity and improve habitat quality, but the effectiveness of subcatchment-scale connectivity restoration on recovery of fish communities is poorly understood. We used a before-after-downstream-upstream methodology to determine the effects of subcatchment-scale connectivity restoration on fishes in a fragmented tributary of the River Wear, Northeast England, between 2013 and 2019. Following restoration (three barriers removed, five barriers fitted with fish passes, two barriers unaltered), riffle habitat increased, fine sediment decreased, and most fish species benefitted. Total fish abundance, comprising seven native species, increased 3 years after the restoration and remained elevated to the end of the study. Mean brown trout (*Salmo trutta*) density increased from 20.9 ± 6.3 to 33.8 ± 16.8 per 100m^2 from 2013 to 2019, with Young-of-Year trout increasing from 10.6 ± 4.6 to 19.8 ± 11.8 per 100m^2 . Connectivity restoration reduced the mean age of trout, suggesting a change to an increased migratory component of the population. Density of bullhead (*Cottus perifretum*), a species with poor dispersal ability, increased from 4.6 ± 2.7 to 32.6 ± 17.9 per 100m^2 over 2013 to 2019. Stone loach (*Barbatula barbatula*), also a less mobile species but tolerant to fine sediment, decreased in abundance where barriers were removed. Atlantic salmon (*Salmo salar*) were absent over the study timescale, despite being common in the Wear, and despite suitable habitat and water quality in the restored subcatchment, suggesting a hysteresis effect. Our findings indicate that, where good water quality exists, restoring river connectivity and hydromorphology at a subcatchment scale is

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beneficial for most native resident and migratory fishes. However, the ecological benefits of connectivity restoration, especially in rivers with many barriers, may take several years to develop. We encourage well-controlled long-term studies reporting the outcomes of large-scale connectivity restoration.

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1. Introduction

Relative to their area, freshwater ecosystems are disproportionately important for biodiversity (Dudgeon et al., 2006; Reid et al., 2019) and ecosystem service provision (Auerbach et al., 2014; Costanza et al., 1997). Rivers have been altered for millennia by humans (Gregory, 2006), but the rate of river ecosystem degradation has increased during the Anthropocene (Meybeck, 2003; Reid et al., 2019). However, this temporal pattern has differed regionally. In large parts of Europe and North America much of the worst damage occurred during the agricultural and industrial revolutions, with widespread river fragmentation by many small dams (Downward and Skinner, 2005; Hall et al., 2011; Lenders et al., 2016), severe pollution (Archer et al., 2003; Meybeck et al., 2018) and fisheries overexploitation (Lenders et al., 2016; Limburg and Waldman, 2009). Subsequent decline of heavy industry and improved effluent treatment have improved water quality, enabling the partial recovery of sensitive indicator species such as Atlantic salmon and trout *Salmo* spp. (Champion, 1991; Le Pichon et al., 2020). Nonetheless, longitudinal river connectivity in Europe is still affected by the large number of redundant river infrastructures (Belletti et al., 2020), including in Great Britain (Jones et al., 2019), which impact fish migration and dispersal, inhibit sediment transport and alter upstream habitat and biotic components upon which fish depend (Carpenter-Bundhoo et al., 2020; Mueller et al., 2011; Sun et al., 2021). So, the restoration of more naturally functioning river ecosystems in post-industrial and other heavily modified rivers typically requires a variety of further actions, including reinstatement of hydrological, geomorphic and biological connectivity and a return to more natural instream and riparian habitats (Bernhardt et al., 2005; Feld et al., 2011; Wohl et al., 2015).

Improving connectivity in rivers is increasingly seen as a priority for supporting the recovery of native fish communities (Mattocks et al., 2017; Mueller et al., 2011; Tummers et al., 2016). Although lateral connectivity restoration is key for fishes in floodplain river reaches (Bolland et al., 2012), most river barrier removal or mitigation seeks to restore longitudinal connectivity, helping to reinstate migration routes for fish species and restore natural hydromorphic and ecological processes (Brown et al., 2013). Several methods have been developed to improve river connectivity, but physical removal of a barrier is considered to be the only feasible method to completely restore both fish passage and river habitat (Birnie-Gauvin et al., 2017a). Barrier removal returns the flow conditions in a previously impounded reach from lentic to lotic, restoring sediment transport, supporting stream habitat complexity and the recovery of lotic fish species and communities (Bednarek, 2001; Birnie-Gauvin et al., 2017b; Burroughs et al., 2010; Fjeldstad et al., 2012; Sun et al., 2021). In some cases, when barrier removal is not feasible due to reasons such as financial costs, flood control, hydropower, water supply, irrigation, and recreation (Kuby et al., 2005), an alternative plan is fish pass construction. However, these are mitigations rather than full solutions (Kemp, 2016), and the efficacy in facilitating fish passage is often low and species-specific (Bunt et al., 2012; Foulds and Lucas, 2013; Noonan et al., 2012).

Within a catchment, a river is often fragmented by multiple barriers, many of which are small (Sun et al., 2020; Belletti et al., 2020), and the cumulative effects on fish movement, distribution and abundance can be stronger as a result of this (Diebel et al., 2015; Lucas et al., 2009). An increased number of barriers causes a greater cumulative extent of impounded, lentic habitat (Birnie-Gauvin et al., 2017a), but also inhibits migration and dispersal, including for upstream-directed recolonisation

by population fragments (Radinger and Wolter, 2014; Tummers et al., 2016; Wilkes et al., 2019). Understanding the effects of connectivity restoration in a catchment with multiple barriers is important for ecologically sensitive river management and conservation of migratory fish species (Branco et al., 2014; Fullerton et al., 2010), but is seldom studied empirically at the catchment or subcatchment scale. Positive impacts of subcatchment connectivity restoration have been observed on brown trout (*Salmo trutta*) smolt abundance in a Danish river (Birnie-Gauvin et al., 2018) and overall fish species richness and abundance in a small tributary in the US (Gardner et al., 2013). Responses to (sub)catchment restoration, even for small streams, can take many years (Feld et al., 2011), yet longer-term studies remain rare within the literature, although a few examples exist for short river reaches (Shirey et al., 2016). Moreover, standardised sampling and careful experimental design over an extended timescale are needed to ensure the accuracy and utility of studies assessing restoration effectiveness, not least because natural systems are subject to stochastic processes which can obscure longer-term trajectories of response (Palmer et al., 2005; Shirey et al., 2016).

This study's overall aim was to evaluate the effects of subcatchment-scale connectivity restoration, and associated hydromorphic naturalisation, on the native fish community of a post-industrial river catchment. We hypothesised that river connectivity restoration increases the abundance and diversity of native stream fishes, especially rheophiles, across a subcatchment. The constituent objectives were to determine: (1) the extent, in terms of fish diversity and abundance, and speed, within a medium-term (2013–2019) ecological timeframe, with which the fish community responds to subcatchment-scale connectivity restoration; and (2) the degree to which barrier removal may give better fish community restoration outcomes than fish pass installation, in the reach immediately upstream of the barrier location.

2. Methods

2.1. Study site

The study area comprised the River Deerness (subcatchment area, 53 km²; Fig. 1) which joins the River Browney (subcatchment area, 75 km²), in turn entering the middle reaches of the River Wear (catchment area, 1321 km²), Northeast England. Prior to the industrial revolution, Atlantic salmon (*Salmo salar*) and anadromous brown ('sea') trout (*Salmo trutta*) were abundant in the Wear (Commissioners for the British fisheries, 1861). The Wear became environmentally degraded due to intensive mining for heavy metals and coal; largescale coal-coking for steel-making; heavy industry; increased river barrier building; and untreated sewage release from urban areas (Sun, 2021). Anadromous salmonids became functionally extinct in the river by the late 19th century (Sun, 2021). Parts of the Wear suffered severe water pollution until the late 1960s (Whitton et al., 1998), when heavy industry declined and water treatment improved (Sun, 2021). Salmon and sea trout populations recovered partially, mostly through natural recolonisation (Fig. S1). The Wear is characterized as a 'salmonid' river, but it is inhabited by approximately 20 native fish species within the families Petromyzontidae, Salmonidae, Anguillidae, Cyprinidae, Nemacheilidae, Cottidae, Gasterosteidae, Percidae and Pleuronectidae (Sun, 2021). Although the river's water quality has improved greatly, parts of the catchment remain impacted by its industrial legacy, particularly due to habitat fragmentation by redundant river barriers (Sun et al., 2020).

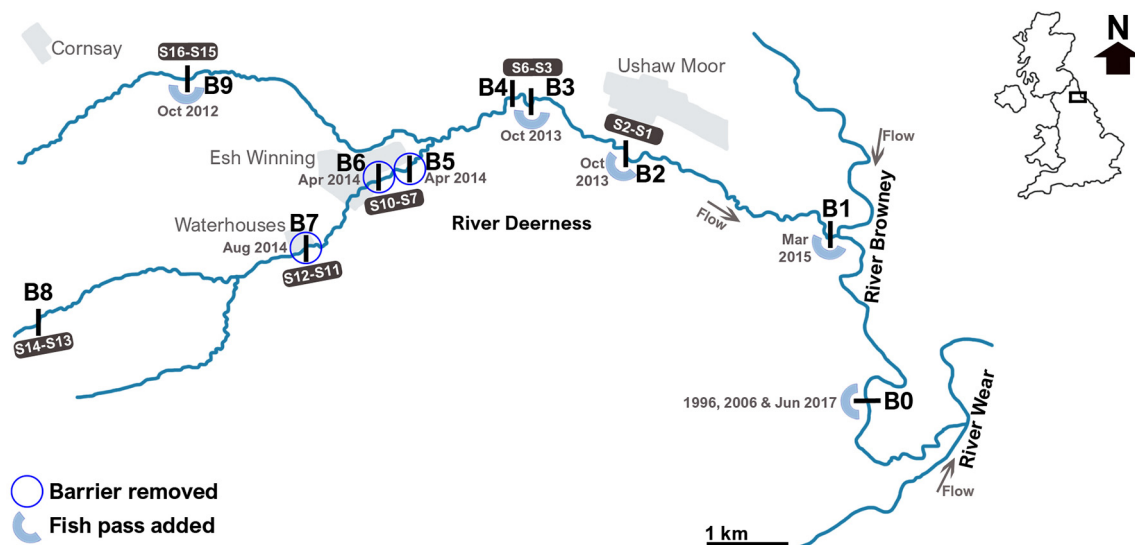


Fig. 1. River Deerness sub-catchment in which connectivity restoration occurred. Locations of in-stream barriers (B0–B9) and fish sampling sites (S1–S16) are shown, together with the dates and methods by which longitudinal reconnection was carried out (further detail in Table S3). Sample sites were in pairs, immediately below and above each barrier. No connectivity restoration occurred at B4 or B8 so these remained ‘control’ sites over the study period. Urban areas close to the stream are shaded grey. The bifurcating tributaries upstream of Waterhouses extend several km further upstream.

The River Deerness originates 285 m above sea level, has a gradient of 12 m km^{-1} over its 18.7 km length and an average discharge of $\sim 0.5 \text{ m}^3 \text{ s}^{-1}$. Land use in the Deerness subcatchment mostly consists of semi-natural woodland, pasture and arable land. Over much of its length, the stream is bordered by native trees, providing overhead cover and underwater root refuges for fish. The stream may have suffered historical undescribed morphological deterioration, but in recent decades it is characterized by pool-riffle-glide sequences with abundant gravel, cobble and boulders, providing good-quality salmonid spawning and nursery habitat (Tummers et al., 2016; Winter et al., 2016). Instream macrophytes are uncommon, but epilithic algae are moderately abundant. The river suffered severe pollution due to coal mining, cokeworks and sewage from the mid-19th Century to the mid-20th Century (Durham Mining Museum, 2020; Emery, 1984). Since the 1970s, water quality in the Deerness has greatly improved (Fig. S2, Table S1).

Under the EC Water Framework Directive's (WFD) assessment criteria (European Commission, 2003), the ecological status of the Deerness was classified as “Poor” in 2009 and 2013 (Environment Agency, 2020a). A deficiency in salmonid numbers and absence of Atlantic salmon in the Deerness were largely attributed to poor fish passage (Environment Agency, 2020a). Water quality for fish in the Deerness is now good (Environment Agency, 2020a), and was consistently good across the study period (Fig. S2, Table S2). In order to improve river connectivity and hydromorphic processes in the Deerness, restoration actions were conducted in 2012 (one site), 2013 (two sites), 2014 (three sites) and 2015 (one site) (Fig. 1). All barriers and their removal/modification (except B1, a 0.2 m high bridge apron, which is an obstacle in low flows only) are described in Tummers et al. (2016) and summarized in Table S3. In the Browney, into which the Deerness runs, upstream passage improvements for salmonids had already been made at B0, a 1.2-m head flow-gauging weir, in 1996 by the addition of two 0.25-m high notched weirs (‘preimpoundments’) downstream, reducing the head of the main weir to 0.7 m, while a bristle-type elver pass was added in 2006 and a Larinier fishway in 2017 (Lothian et al., 2020).

2.2. Study design

At sub-catchment scale, a before–after (BA) study design was used, where the status of each barrier, and associated sample sites, represents

‘before–after’ (before: before restoration; after: after restoration). At a subcatchment scale, summer 2013 samples represented ‘before’ conditions, summer 2014 samples represented ‘during’, and summer 2015–2019 represented ‘after’. It has been argued above that restoration of fish communities in heavily obstructed rivers, may require reconnection at many barriers (due to cumulative barrier impacts). Therefore, the connectivity restoration treatment level may be argued to be at the extended reach, or whole subcatchment level, rather than locally at barriers. In that regard, the only evidence of treatment effect at the subcatchment level that could be evaluated in this study is the before–after response, as no nearby subcatchments provided equivalent tributaries, unaltered over the study timescale, that could be used as barrier ‘control’ and unaltered ‘reference’ catchments.

Because our objectives included understanding the local effects of fish passes and barrier removals on habitat, species composition and fish abundance, we sampled pairs of sites immediately upstream and downstream of barrier locations. A downstream–upstream–control–impact (DUCI) design was performed to compare the effects between barrier removal and fish pass installation on habitat characteristics, and on fish abundance, after connectivity restoration. Further analyses determined interaction effects between site location (upstream and downstream) and three treatments: 1) no mitigation on barrier (control), 2) fish pass installation, and 3) barrier removal, on fish species abundance, but this was not possible for habitat due to insufficient ‘control’ data.

2.3. Habitat surveys

River habitat surveys were carried out, using the Scottish Fisheries Coordination Centre methodology, a standardised method of recording river habitat in a manner relevant to fishes (SFCC, 2007). A total of 16 sites (ranging between 60 and 80 m long, but constant for each site over the study duration) were selected, distributed in pairs, immediately upstream and downstream of each of the original barrier locations B2–B9 (Fig. 1). B1 was not identified as a potential barrier initially, because it only affects fish dispersal during very low flows (J. Sun, pers. obs.), thus it remained unsampled throughout the study. Each site was surveyed in summer 2013, 2014, 2018 and 2019 at base water flows ($\sim Q_{95}–Q_{80}$). Because barrier removal is most likely to alter flow patterns and sediment transport (Bednarek, 2001; Sun et al., 2021), habitat elements considered here comprise flow types and sediment

characteristics. Stream flow type at each site was apportioned by percentage of run, riffle, pool and glide. The percentage river bed substrate composition in each site was visually and manually assessed over the full length and width of each site, using an approximation to the Wentworth-scale: boulder (>256 mm), cobble (64–256 mm), gravel (2–64 mm), sand (0.06–2 mm) and silt (<0.06 mm).

2.4. Fish surveys

Fish were surveyed each summer, 2013–2019, at base water flows at the 16 sites described in Section 2.3, including on the newly built bypass at B3. Otherwise, the location and length of each site stayed the same during the study period. Because a fish pass was installed at B9 in October 2012, fish communities were sampled immediately upstream and downstream a month beforehand, instead of the summer sampling (Tummers et al., 2016), after which sampling reverted to summer. Each fish survey site (60–80 m long, identical to habitat survey sites) contained multiple mesohabitats, so as to increase the possibility of sampling all species of fish with different mesohabitat preferences. Quantitative sampling was carried out by electrofishing using the three-pass 'depletion' method (Reynolds and Kolz, 2012), employing 4-mm mesh stopnets at the boundaries of each fished section. Sampling of the 2–10-m wide channel was done by wading with a single anode, operated with a bankside generator and control box (Honda EU10i, Electracatch WFC1, ~200 V). Fish removed from each pass were kept in separate aerated containers, after which the catches were processed separately. Fish were identified, measured and returned to the capture location after processing. Fish were sampled in summer (typically July and August, when young-of-year (YoY) salmonid fry are large enough to be sampled effectively). In addition, upstream of B9, additional survey lengths were added progressively further upstream to record the extent of colonization of bullhead in subsequent years (single pass fishing, up to 1 km above the last positive detection location; Tummers et al., 2016).

2.5. Data analysis

Densities of each fish species at each site were calculated using Carle and Strub's K-pass removal method, with the R (version 3.6.1, R Core Team, 2020) package 'FSA' (Ogle, 2020). Capture efficiencies for three ecological types of fish: solitary midwater (brown trout), solitary benthic cryptic (bullhead, *Cottus perifretum*) and schooling midwater (common minnow *Phoxinus phoxinus*), were calculated. The mean \pm SD capture efficiency (%) of three-pass fishing was 92.6 ± 4.7 for YoY trout; 96.2 ± 2.3 for older trout; 89.8 ± 8.1 for bullhead and 91.8 ± 5.6 for minnow in the Deerness between 2013 and 2019. Total fish species density was obtained by summing individual species densities obtained from Carle and Strub estimates. Fish density data were fourth-root transformed to meet assumptions of normality before conducting the following analysis (Boys et al., 2012). A national abundance-quality grading system for brown trout (from Grade A = excellent to Grade F = fishless), generated from approximately 1000 reference sites across England and Wales (Mainstone et al., 1994) was used to assess the relative quality of Deerness sites with regard to YoY and older trout and changes over time.

All statistical analysis were conducted in R. Permutational multivariate analysis of variance (PERMANOVA) was used to determine changes in the fish communities, flow types and substrate composition through the time course of and following the restoration work, and the differences between paired upstream and downstream sites, using the R 'Vegan' package (Oksanen et al., 2019). If significant differences in fish communities were found, a similarity percentage (SIMPER) analysis, based on the decomposition of Bray-Curtis dissimilarity index (Clarke, 1993), was used to identify which species contributed more dissimilarity in fish abundance among study sites. Spearman's rank correlation was used to investigate the relationship between fish species richness

and distance from the Deerness confluence, as well as between fish species richness and sampling year. Linear Mixed-effects Modelling (LMM) was performed to analyse the subcatchment scale changes in fish density, flow and substrate composition using the 'lme4' and 'lmerTest' package (Bates et al., 2015; Kuznetsova et al., 2017). Site was used as a random factor when comparing the subcatchment scale changes. Flow and substrate data were $\log(x + 1)$ transformed to meet assumptions of normality before conducting the LMM analysis. The post-hoc Tukey's multiple comparison test was performed to analyse the differences in abundance of each species and total fish density between each study site, using the 'multcomp' package (Hothorn et al., 2020).

Linear Mixed-effects Modelling was employed to determine interaction effects between site location (upstream and downstream) and three treatments (no mitigation on barrier [control]; fish pass installation; barrier removal) on fish density after the restoration (2015–2019). Sampling year was used as a random factor in this model. Additional LMM analyses were conducted to test the difference in substrate and habitat percentage coverage between barrier removal and fish pass treatments. All paired 'upstream and downstream' data were included for 2018 and 2019, but insufficient control site data across those 2 years precluded incorporation of Controls in that comparison.

Based on frequency distributions of lengths (YoY: Year 2013–17, length < 90 mm; Year 2018–19, length < 80 mm; Older: Year 2013–17, length \geq 90 mm; Year 2018–19, length \geq 80 mm), trout sampled were split into YoY trout (age 0+) and older trout (age 1+ and older). This enabled year-to-year fluctuations in recruitment to be analysed by LMM. The Kruskal-Wallis *H* Test was used to test for a difference in trout length (irrespective of age) between study years.

3. Results

3.1. Aquatic habitat

Across all sites, the proportion of silt (mean \pm SD) decreased from $13.1 \pm 5.6\%$ to $0.6 \pm 2.4\%$, and sand decreased from $21.9 \pm 12.2\%$ to $8.4 \pm 6.8\%$, between 2013 (pre-intervention) and 2019 (Figs. 2, S3). The proportion of gravel slightly increased from $30.0 \pm 7.9\%$ to $35.9 \pm 17.2\%$, and cobble increased from $22.2 \pm 7.7\%$ to $32.5 \pm 16.0\%$ between 2013 and 2019. The overall substrate composition in 2018 differed from that in 2013 (PERMANOVA, $F = 80.86$, $P < 0.001$), and did not change further in 2019. In 2013, flow type comprised glide ($40.6 \pm 8.1\%$) with slightly lower proportions of riffle and pool (Fig. 2). The overall flow type did not change across the study period (PERMANOVA, $P > 0.05$ in all cases), but the proportion of riffle increased from $28.8 \pm 14.0\%$ to $47.5 \pm 21.3\%$ between 2013 and 2019 (Fig. 2), and became the majority flow type at 9/16 sites (Fig. S3). Following restoration, sandy substrate coverage was lower where barriers were removed than where fish passes were installed (LMM, $F_{1,21} = 6.51$, $P = 0.019$). In addition, the proportion of riffle habitat in the barrier-removed sites was significantly higher compared with fish pass sites after the restoration (LMM, $F_{1,22} = 5.46$, $P = 0.029$). No significant differences were found in other substrate or flow-type components between fish pass and barrier-removal treatments (LMM, $P > 0.05$ in all cases).

3.2. Fish community and abundance pre- and post-connectivity restoration

The Deerness fish community was unchanged between the pre-intervention year (2013) and remaining years (PERMANOVA, $P > 0.05$ in all cases). For each connectivity-restored site (PERMANOVA, $P > 0.05$ in all cases) as well as between control sites S5 and S6 at unmodified Barrier 4 (PERMANOVA, $F = 4.5$, $P = 0.21$), no differences in fish community were found between upstream and downstream post restoration. A difference in fish community was observed between sites S13 and S14 at unmodified Barrier 8 (PERMANOVA, $F = 36.44$, $P = 0.001$). Bullhead, minnow and stone loach contributed 90.6% dissimilarity in

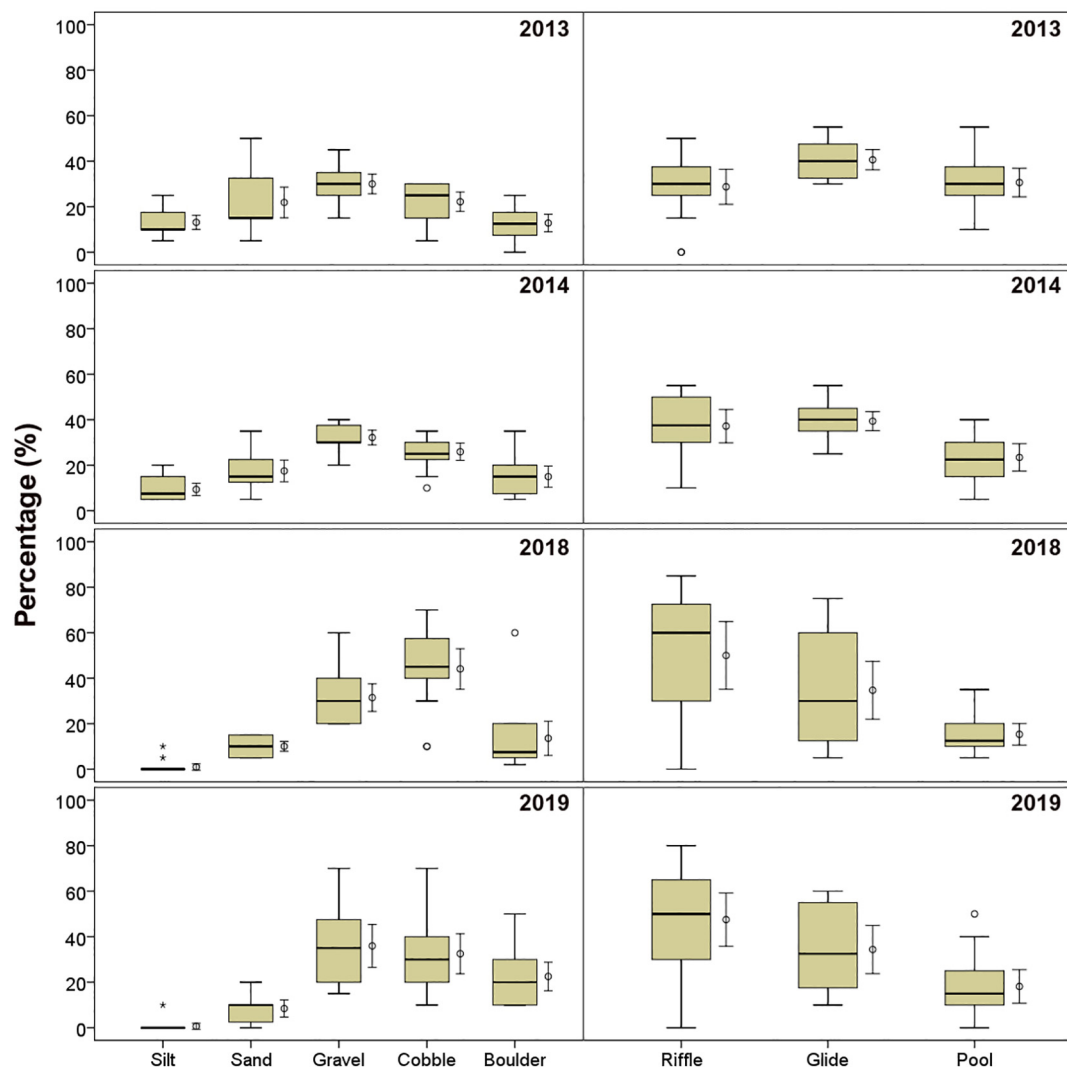


Fig. 2. Habitat characteristics at each site before (2013*), during (2014), and after (2018, 2019), connectivity restoration. Left panel: substrate composition. Right panel: flow type composition. * Fish pass installed at S15-16 in October 2012; all remaining Deerness subcatchment connectivity restoration measures occurred between October 2013 and March 2015. Box plots show range, outliers, lower quartile, median, upper quartile. Vertical lines with dot show 95% CI and mean.

the fish communities between S13 and S14, these species being absent from S14 over the entire study period.

Eight fish species were caught during the study, with brown trout the predominant species before the restoration (i.e. summer 2013) (Fig. 3). Atlantic salmon were not recorded in any year. Bullhead, minnow and stone loach (*Barbatula barbatula*) were present at most sites, typically at slightly lower abundance than brown trout between 2013 and 2019 (Fig. 3). European eel (*Anguilla anguilla*) were present at a very low density. European grayling (*Thymallus thymallus*, $n = 2$) and non-native common carp (*Cyprinus carpio*, $n = 1$) were excluded from analyses due to their low abundance ($<0.01\%$ of total fish caught). Since 2016, three-spined stickleback (*Gasterosteus aculeatus*) appeared in catches, particularly at sites further downstream. The greatest species richness occurred at the downstream-most survey sites, and reduced upstream (Fig. 2; Spearman's correlation, $r_s = -0.904$, $P < 0.001$). For the lower part of the river (S1-S6) there was no correlation between species richness and year (median species richness, 2013 = 4.5, 2019 = 5, $P > 0.05$). For the upper part of the river (S7-S16), there was a negative correlation between species richness and year (median species richness, 2013 = 4, 2019 = 3, Spearman's correlation, $r_s = -0.44$, $P < 0.001$). S14 (upstream of barrier control site B8) was inhabited only by brown trout over the full duration of study, even though up to five species were recorded 100 m downstream at S13

(Fig. 3). The number of species at S13 declined to just two species, brown trout and bullhead, in 2017-2019.

At the subcatchment level, total fish (all species combined) abundance differed between years (Fig. 4, LMM, $F_{6,90} = 13.26$, $P < 0.001$). Total fish densities in 2013, 2014 and 2015 were lower than in 2017, 2018 and 2019 (paired post hoc, $P < 0.001$ in all cases). Total fish density in 2016 was lower than in 2018 and 2019 (paired post hoc, $P = 0.02$ in both cases). Trout, bullhead, stone loach, three-spined stickleback and eel abundance changed during the study (Fig. 4, Table 1; LMM, $P < 0.05$ in all cases). All increased, except for stone loach, which decreased in abundance since 2016 (Fig. 4, Table 1).

Overall, both YoY and older trout abundance increased during the study period (LMM, YoY, $P = 0.04$; older, $P < 0.001$; Table 1). The lowest brown trout density (mean \pm SD; 19.7 ± 6.5 per 100m^2) occurred in 2015, and the highest (53.3 ± 47.8 per 100m^2) in 2018 (Fig. 4). Trout densities in 2013, 2014, 2015 and 2016 were lower than in 2017 and 2018 (Table 2). The YoY trout density increased from 10.6 ± 4.6 in 2013 to 19.8 ± 11.8 per 100m^2 in 2019 (Fig. S4), indicating increased reproductive success since the start of connectivity restoration. From the national abundance-quality grading system for brown trout, YoY trout occurrence in the top two grades A and B quadrupled by 2017-2019 and older trout doubled over the same period (Table S4). By contrast one to two sites reduced to abundance-quality ratings E-F over the

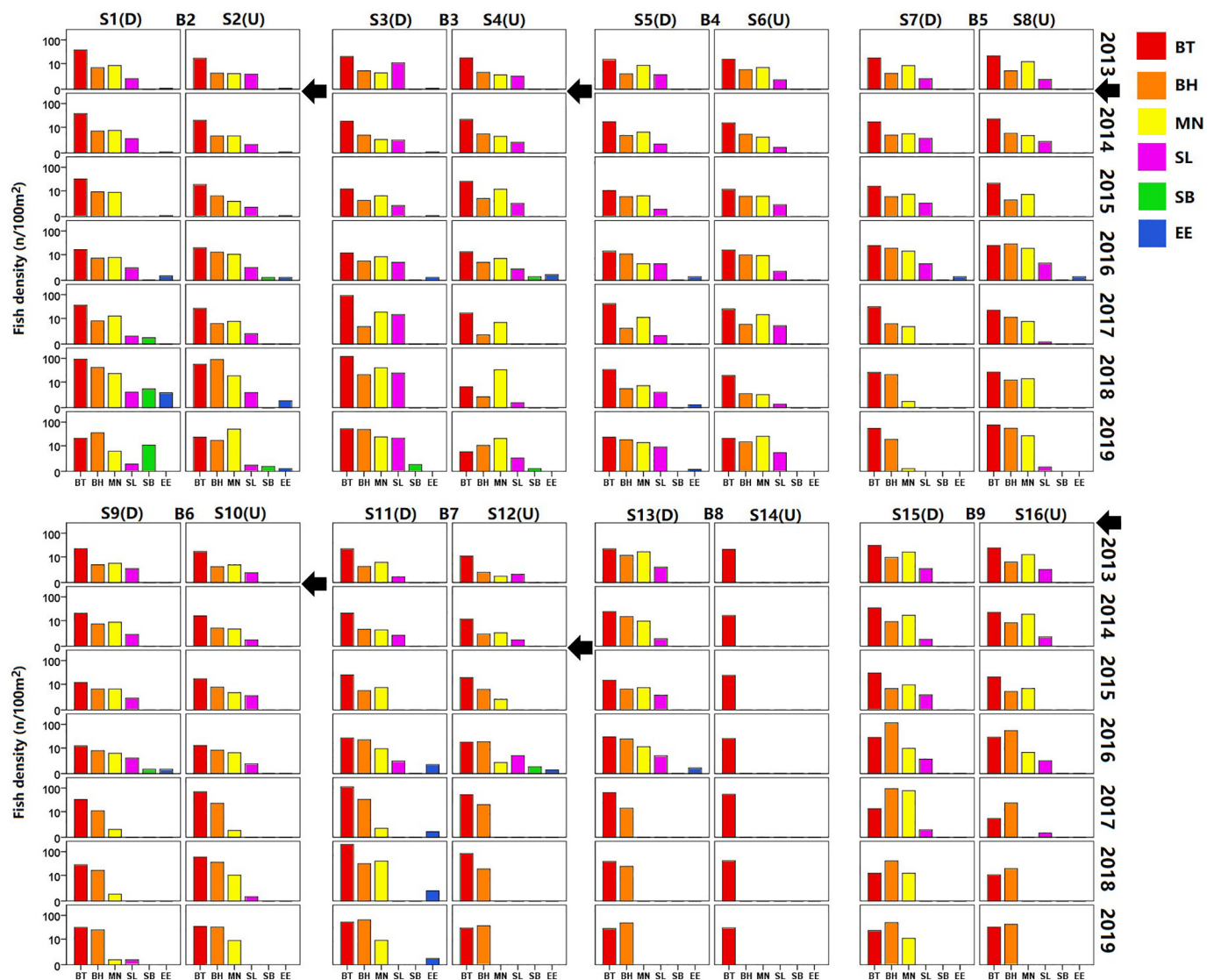


Fig. 3. Abundance of each fish species (note log scale) at each site during the study period. D and U: site located immediately downstream and upstream of a barrier, respectively. BT: brown trout, BH: bullhead, MN: common minnow, SL: stone loach, SB: three-spined stickleback, EE: European eel. Pre-restoration data for S15 and S16 are available for 2012 (see Tummers et al., 2016) but not presented here. The arrows indicate the year of connectivity restoration at each site, relative to timing of summer surveys.

period 2013–2019. Median trout length decreased across the sampling periods (Fig. 5; Kruskal-Wallis H Test, $\chi^2(6) = 332.72$, $P < 0.001$). In 2013–2015 four length modes were apparent (indicative of ages 0+ to 3+), but from 2016 to 2019 only two length modes were evident (0+ and 1+) (Fig. 5).

Bullhead abundance increased across most sites since 2016 (Fig. 3). Bullhead densities in 2013, 2014 and 2015 were lower than those in 2018 and 2019 (Table 2; $P < 0.001$ in all cases, Fig. 4). Bullheads were absent upstream of B9, before the connectivity-restoration in October 2012 (Tummers et al., 2016) but following fish pass construction at B9, they recolonized the upstream reach at a rate of over 100 m every year. Six years post-restoration (summer 2018), they had recolonized 798 m upstream of B9. Stone loach abundance declined in S7–S16 from 2017 onwards, with loach being absent or at negligible densities (Table 2; paired post hoc, $P < 0.05$ in all cases). No change in minnow abundance occurred during the study period (Table 1). Eel were mostly caught in downstream sites (S1–S3) between 2013 and 2015, but density increased in 2016 (Table 2; paired post hoc, $P < 0.001$); and they dispersed as far as S13. By 2017–2019 eel remained at low densities, but were more widespread than over the period 2013–2015.

3.3. Barrier removal vs fish pass installation effects on fish

During the period 2017–2019, a significant interaction effect occurred between the three connectivity treatments (no mitigation, fish pass installation, and barrier removal) and site location (upstream and downstream) for YoY trout density (LMM, $F_{2,42} = 4.84$, $P = 0.013$). YoY trout increased in abundance immediately upstream of where barriers had been removed (S8, S10 and S12). By contrast, YoY trout in several of the impounded sites (S2 and S4) with fish passes were mostly at a low abundance (Fig. 6). No interaction effects were found in both older trout and total trout density (LMM, $P > 0.05$ in both cases). Changes in local densities of YoY and older trout over the study period are illustrated in Fig. S5. Over the period 2017–2019, a significant interaction effect between the three connectivity treatments and site location was found for bullhead density (LMM, $F_{2,40} = 5.21$, $P < 0.001$). Bullhead abundance increased more at barrier removal sites, compared with impounded sites with fish passes and no-mitigation control sites. No interaction effects were found in remaining species (LMM, $P > 0.05$ in all cases).

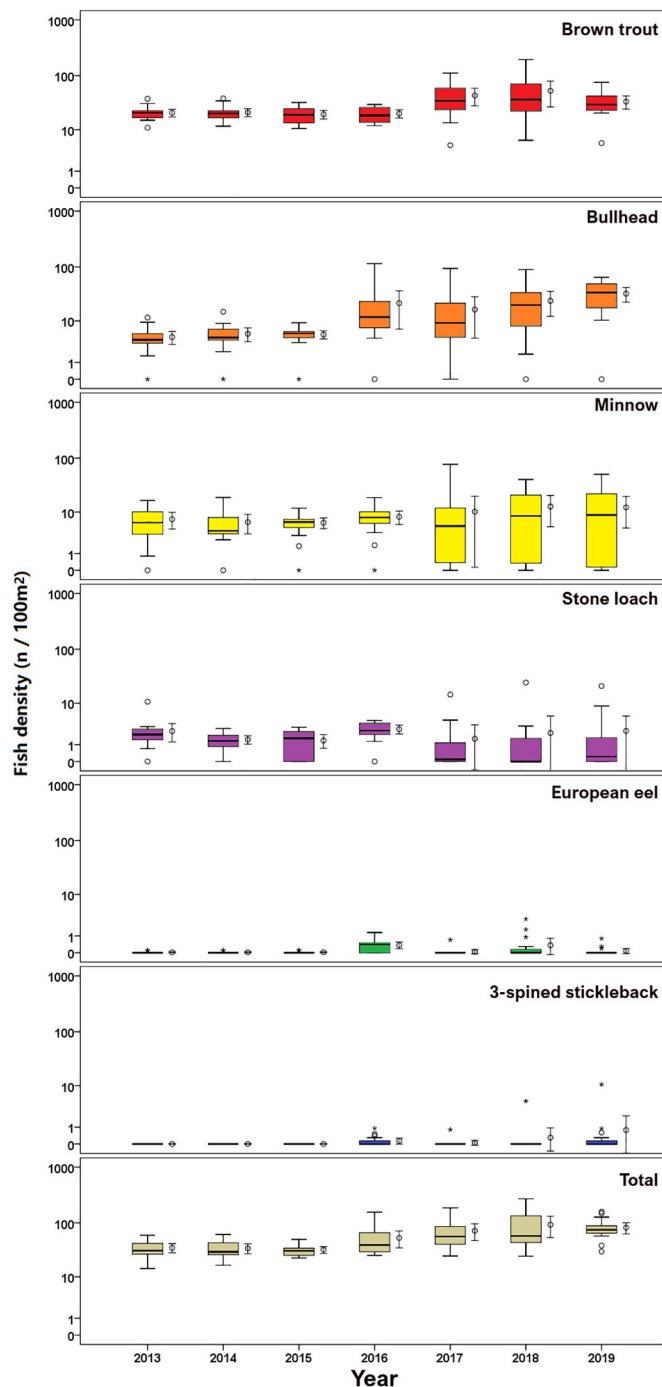


Fig. 4. Fish species' density (per 100 m²) across years for the River Deerness subcatchment. Box plots show range, outliers, lower quartile, median, upper quartile. Vertical lines with dot show 95% CI and mean. Summer 2013 represents pre-restoration, 2014 during restoration and 2015-19 post-restoration.

4. Discussion

This study suggests that connectivity restoration which lessened impoundment facilitated natural hydromorphic processes, including flushing of fine sediment, and increases in coarse substrate and riffle habitat in a subcatchment, even when just a proportion of barriers were removed. This study supports parts of our hypothesis, in that the abundance and distribution of several migratory and river-resident rheophilic fish species (e.g. brown trout, bullhead) increased in response to a combination of more natural hydromorphic conditions and increased connectivity, although these changes in abundance and

Table 1

Change of fish density (Linear Mixed-effects Modelling) in the River Deerness across years.

| Species | Mean square | df | F | P | Trend |
|----------|-------------|------|-------|--------|-------|
| Total | 1.146 | 6,90 | 13.26 | <0.001 | ↑ |
| BT | 0.561 | 6,90 | 6.05 | <0.001 | ↑ |
| BT YoY | 0.351 | 6,90 | 2.22 | 0.04 | ↑ |
| BT Older | 0.306 | 6,90 | 5.06 | <0.001 | ↑ |
| BH | 1.692 | 6,90 | 18.61 | <0.001 | ↑ |
| MN | 0.166 | 6,90 | 0.66 | 0.68 | – |
| SL | 1.268 | 6,90 | 6.65 | <0.001 | ↓ |
| SB | 0.193 | 6,90 | 2.64 | 0.02 | – |
| EE | 0.523 | 6,90 | 8.17 | <0.001 | ↑ |

BT: brown trout, BH: bullhead, MN: common minnow, SL: stone loach, SB: three-spined stickleback, EE: European eel.

distribution took 3–4 years to develop. On the other hand, parts of the hypothesis are refuted by the result, since fish diversity across the subcatchment was either not affected (lower Deerness) or negatively affected (upper Deerness) over the study duration. Although we might have expected a more natural stream channel environment to support greater native fish diversity, it benefitted rheophilic brown trout and bullhead most. There was no evidence that the fish community changed at the subcatchment-scale after connectivity restoration, but local differences were evident. Brown trout, bullhead, European eel and three-spined stickleback increased in abundance and stone loach became less abundant. Although there was an expectation that Atlantic salmon would begin to colonize the reconnected stream, this did not happen over the 7-year study period.

The study stream's moderate gradient (12 m km⁻¹) and rapid hydrological response to rainfall result in a naturally dynamic hydromorphic environment, typical of 'spate streams' and resulting in periodic sediment movement locally. Improved river connectivity due to river restoration has enhanced and further naturalised this (Wohl et al., 2015). However, it is evident from observations of reduced fine sediment at control sites in the upper reaches, such as B8, that not all of the habitat changes observed were the result of connectivity restoration. Instead, across the subcatchment, natural hydromorphic processes have been facilitated by restoration actions, as observed in other studies (Feld et al., 2011; Shirey et al., 2016; Sun et al., 2021).

Following connectivity restoration and habitat improvement in the Deerness, overall fish abundance increased during 2017–2019, with particular contributions from the rheophilic and lithophilous specialists, brown trout and bullhead. Tummers et al. (2016) evidenced that

Table 2

Paired post hoc test of Linear Mixed-effects Modelling (Tukey's multiple comparison) showing significant differences in different fish species densities in the Deerness during the study period (2013–2019).

| Species | Year | Z | P |
|-------------|-------------|-------|---------|
| Brown trout | 2013 - 2017 | 3.18 | 0.025 |
| | 2013 - 2018 | 3.72 | 0.004 |
| | 2014 - 2017 | 3.11 | 0.031 |
| | 2014 - 2018 | 3.65 | 0.005 |
| | 2015 - 2017 | 3.53 | 0.008 |
| | 2015 - 2018 | 4.07 | < 0.001 |
| | 2016 - 2017 | 3.36 | 0.014 |
| Bullhead | 2016 - 2018 | 3.90 | 0.002 |
| | 2013 - 2018 | 5.62 | <0.001 |
| | 2013 - 2019 | 8.00 | <0.001 |
| | 2014 - 2018 | 5.09 | <0.001 |
| | 2014 - 2019 | 7.47 | <0.001 |
| | 2015 - 2018 | 5.01 | <0.001 |
| Stone loach | 2015 - 2019 | 7.39 | <0.001 |
| | 2016 - 2017 | -4.16 | <0.001 |
| | 2016 - 2018 | -4.32 | <0.001 |
| | 2016 - 2019 | -3.69 | 0.004 |
| Eel | 2013 - 2016 | 5.29 | <0.001 |
| | 2014 - 2016 | 5.29 | <0.001 |
| | 2015 - 2016 | 5.29 | <0.001 |

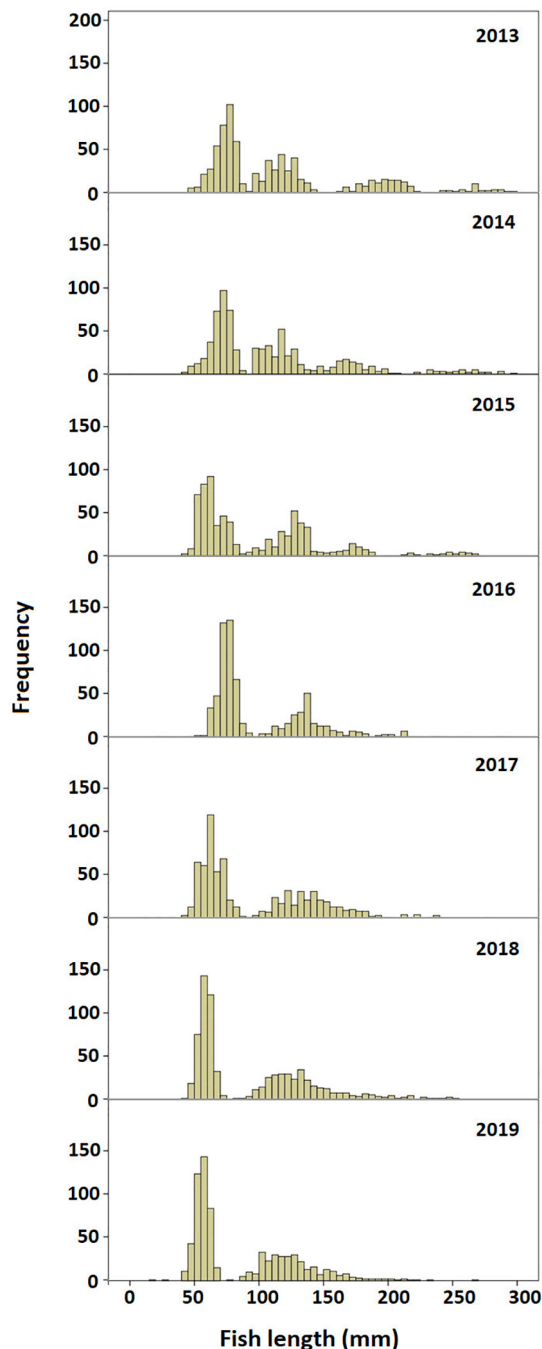


Fig. 5. Length-frequency distribution of brown trout from the Deerness subcatchment (all study sites combined) during the study period 2013–2019.

connectivity restoration in the Deerness increased passage and dispersal of these species, but found no increase in their abundance within the first 2 years of restoration for the same survey sections described here. Unlike the quick recovery of brown trout after a small dam removal in a Danish river (Birnie-Gauvin et al., 2017b), the trout population in the Deerness took 4 years to exhibit a marked increase. Although neither barrier-impacted ‘control’ nor barrier-free ‘reference’ subcatchments were available for comparison in our study, trout density remained relatively stable over years at control sites B4 and B8, but increased following restoration actions at most other sites, especially B5–B7, which were removed. This, combined with significantly increased YoY trout densities post-restoration suggests that the increase in fish density is a genuine response to connectivity restoration and

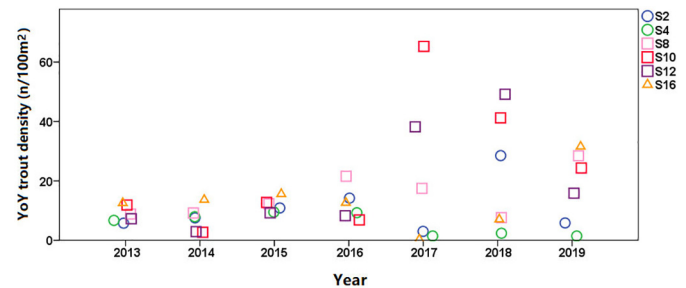


Fig. 6. Young-of-the-year trout density (per 100 m²) changes immediately upstream of connectivity-restored sites in the River Deerness subcatchment. Circle: sites where a fish pass was installed but which retained ponding upstream of the barrier; Square: sites immediately upstream of barrier, where the barrier was fully removed; Triangle: site at which a fish pass was installed but where there was no ponding immediately upstream of the former barrier. All restoration measures complete before 2015 sampling.

improved habitat for rheophilic fishes, rather than an outcome of temporal stochasticity or local redistribution of the same fish. Our study would also have benefitted from sampling of ‘reference’ sites distant from the barriers studied, and we are unable to confirm that the observed changes in fish abundance extended widely between obstacle sites, although the increased abundance at sites where barriers were removed suggests this would be so.

The observed recruitment lag time for trout in the Deerness may be because the generation time of brown trout is a minimum of 2–3 years in this stream (M. Lucas, pers. obs.), and none of the first four downstream barriers were fully removed, so the presence of these barriers may still affect the penetration of migrant trout spawners and resultant egg deposition to some degree. The observed increases in Deerness trout abundance occurred despite a possible decline in River Wear sea trout abundance over the same timescale (Fig. S1). Stream habitat changes benefitting most rheophilic, lithophilous species were apparent by 2018, although surveys were only carried out in 2013, 2014, 2018 and 2019. The absence of control or reference catchments in this study, the situation in most subcatchment scale restoration studies (Feld et al., 2011) makes it unclear as to the degree to which barrier removal was responsible for a transition towards more riffle habitat and larger sediment sizes, but the observed pattern is consistent with barrier removals elsewhere (Bednarek, 2001; Sun et al., 2021). An additional constraint of our study, common to most restoration monitoring studies (Feld et al., 2011), was the limited period of sampling prior to restoration, precluding identification of stochastic temporal variability in fish abundance beforehand; we recommend, wherever possible, that 3–4 years of pre-restoration data is gathered using the same sites and methodology.

The degree to which subcatchment reconnection has enabled the restoration of more natural fish communities and species abundance, can be gauged relative to reference conditions (Palmer et al., 2005). For post-industrial streams and rivers, like that studied, the reference condition refers to the state before large-scale industrial disturbances. This is poorly known for the Deerness, except that brown trout and Atlantic salmon would have been key fish community components. In the absence of better information, reference communities can be indicated by the species in the lowest section close to the confluence or from a nearby free-flowing stream (Mims and Olden, 2013; Woolsey et al., 2007). With regard to abundance of indicator species such as brown trout, a better perspective can be obtained from considering these against reference conditions from a large sample size of sites. Such reference assessments of expected abundance of salmonid indicator species in good habitat conditions have been developed across Western Europe, often by classification into percentiles of abundance, typically referenced against correlated habitat criteria (Aprahamian et al., 2006; Forseth et al., 2013; Romakkaniemi et al., 2003). For the Deerness, the national trout and salmon abundance-grading system (Mainstone et al., 1994) shows that overall it moved from ‘average’ to ‘good-

excellent' condition for trout over 7 years, but remained fishless for salmon (Table S4).

After restoration, the increased proportion of riffle habitat along with the reduction of silt and sand substrates across the Deerness sub-catchment suggests a recovery of the sediment transport process, which led to an improvement of the in-stream habitat for rheophilic fish species. This was particularly apparent at S7-S12 in the reach where three barriers (B5-B7) were removed. Strongly increased YoY trout abundance across the barrier-removed reach suggests barrier removal successfully restored the river connectivity and improved access to, and availability of, high-quality rearing habitat for trout fry and parr. The length-frequency distribution of trout shifted from four clear length modes (putatively Age 0+, 1+, 2+ and 3+) in 2013 to two length modes (Age 0+ and 1+) in 2016-2019. It is very likely this reflects an increase in the proportion of migratory Deerness trout, emigrating to the main river or to sea (principally at Age 2) after the connectivity restoration. A substantial proportion of Deerness trout spawners are sea trout (Tummers et al., 2016; Lothian et al., 2020) and autumn and spring emigrations of Deerness trout juveniles have been recorded (Winter et al., 2016), although historical records of abundance are available for neither. A similar pattern of trout population response to connectivity restoration was observed in the River Villestrup, Denmark after six weirs were removed (Birnie-Gauvin et al., 2018).

The migratory behaviour of brown trout is under partial genetic control and has a high heritability, but there is a strong environmental component influencing migration tendency (Ferguson, 2006; Ferguson et al., 2019). Genetic control is well developed in resident salmonid populations living in habitats where emigration is inhibited (Ferguson, 2006). Longitudinal connectivity restoration increases the relative abundance of migrant phenotype trout due to its increased fitness under those conditions (Ferguson et al., 2019; Northcote, 1992). The large increase in juvenile trout abundance in the Deerness since 2017 may potentially have increased intraspecific competition for food and habitat (Jonsson and Jonsson, 2006). The availability of food strongly influences the growth of brown trout (Elliott, 1976), as well as the tendency for trout parr to smoltify or remain resident in the river (Ferguson et al., 2019; Olsson et al., 2006). Migration to sea increases the feeding opportunities, and leads to increased fecundity, particularly for female salmonids (Ferguson, 2006). It is suggested that these combined factors have led to the progressive reduction of resident brown trout abundance but increased the migratory sea trout abundance in the Deerness.

In 2016-2018, the study area suffered relatively dry weather conditions during the trout pre-spawning and spawning seasons (September-December) compared with 2012-2013 (Fig. S6). Tummers et al. (2016) showed restricted upstream access of adult sea trout in the Browney-Deerness subcatchment in autumn 2014. It was expected that low autumn flows in 2016-2018 could result in poor spawner access and egg deposition and resultant low fry densities in the following years. However, both YoY and older trout abundance were elevated in 2017-2019 compared to before. This suggests that, for the range of flows observed, adult trout could still access upstream spawning habitat during relatively dry autumns and that spawnings were successful.

We found that YoY trout increased to greater densities at sites immediately upstream of barriers that had been removed than those provided with fishways, and that habitat at these sites (S8, 10 and 12) became more suited to YoY trout, with increased riffle habitat in particular. This suggests that barrier removal is a more effective way in locally restoring juvenile trout abundance in the upstream section compared with fish pass construction. Building fish passes only mitigates the disconnection of fish passage and is unable to restore the habitat immediately upstream of the barrier towards its natural state (Birnie-Gauvin et al., 2017a; Silva et al., 2018). The spatial extent of artificially impounded habitat impact on the Deerness (< 60 m long) and other moderate-gradient streams is less than for low-gradient streams such as Danish trout streams (Birnie-Gauvin et al., 2017a). Brown trout spawn in gravel where sufficient flow permeates to oxygenate the

developing eggs and, after emergence, trout fry inhabit nearby shallow riffles (Armstrong et al., 2003; Shirvell and Dungey, 1983). Larger brown trout juveniles often occupy shallow and slow-flowing areas but may move to deeper areas as they grow (Armstrong et al., 2003). Even small barriers can inhibit movement of fine sediments which can lower survival rates of trout eggs and inhibit the emergence of fry (Louhi et al., 2008; Soulsby et al., 2001). At S2 and S4, upstream of B1 and B2 respectively, stream habitat was dominated by slow flowing deep glides (> 1 m deep), and both barriers retained fine sand (mixed with gravel/cobble) immediately upstream, suitable only for large parr and resident adult trout. So, YoY trout at S2 and S4 were still at low abundance six years after the restoration, in contrast with S8, S10 and S12. It is also apparent that following installation of the nature like bypass at B2, the downstream site, S3, became dominated by cobble riffle and produced very high densities of YoY trout from 2017 onwards.

Although Atlantic salmon are now abundant in the River Wear (Fig. S1), they were absent from the Deerness over 2013-2019, and only low densities occurred in the Browney (Environment Agency, 2020b). Although Atlantic salmon often spawn in main river channels and larger tributaries, they also utilize tributaries as small or smaller than the Deerness (Jonsson and Jonsson, 2011; Louhi et al., 2008). Water quality (Table S2) and habitat condition (Section 2.2) in the Deerness were consistently good over the period 2012-2019, so the continued absence of salmon seems to be due to a hysteresis effect. Atlantic salmon recolonization of rivers from nearby and distant stocks, through straying, is well established (Perrier et al., 2009; Vasemägi et al., 2001). Nevertheless, the philopatric behaviour of Atlantic salmon limits their dispersal (Jonsson and Jonsson, 2011; Hendry et al., 2004) so a stream without salmon juveniles, is unlikely to be visited by spawners, particularly if the watershed's population(s) is well below carrying capacity and resultant competition is low.

Bullhead abundance increased steadily during the study period. Like trout, bullhead rely on fast-flowing streams with little sand and silt, but they spawn under cobbles and boulders (Knaepkens et al., 2002). Removal of barriers and reinstatement of high-quality fluvial habitat is expected to benefit spawning, growth and survival of bullhead (Uttinger et al., 2008). However, studies have shown no relationship between water depth and bullhead density (Tomlinson and Perrow, 2003; Uttinger et al., 2008) and large substrate (cobble, boulder) still persisted in areas upstream of barriers. So, even in S2 and S4, immediately upstream of B2 and B3 respectively, bullhead abundance increased. Due to their poor swimming and lack of jumping ability, bullhead cannot ascend river barriers higher than 18-20 cm (Uttinger et al., 2008), so bullhead remained downstream of control B8, during the study period. Nevertheless, nature-like passes can be effective in facilitating upstream and downstream movement of bullhead (Tummers et al., 2016), enabling upstream recolonization, as at B9. Opposite to brown trout and bullhead, the stone loach population decreased in S7-S16 since 2017. Stone loach are more tolerant of sand-silt habitat than salmonids and bullhead (Kukula and Bylak, 2020), so previously benefitted from ponded areas upstream of barriers, three of which (B5-B7) were removed in the upper Deerness in 2014. However, stone loach disappeared downstream of the B8 control site from 2017 onwards, possibly due to the change to more riffle-dominated habitat (Fig. S3) or due to stochastic effects on their abundance within the study system. Three-spined stickleback has been found in the study sites since 2016. The stickleback population probably originated from small ponds and ditches and persisted in the stream channel due to increased connectivity. Three-spined stickleback caught in the Deerness were identified as the inland freshwater-resident form rather than the anadromous form, due to their weak lateral armouring and small body size (~3 cm) (Lucas and Baras, 2001). To date in our study we have seen negligible evidence of connectivity restoration in the Deerness facilitating colonization by non-native fish species, but clearly this is a risk which needs to be managed sensitively on a catchment-specific basis (Jones et al., 2021; Terêncio et al., 2021).

This study demonstrates the extent to which catchment-scale connectivity restoration, with associated hydromorphic naturalisation, can affect the abundance and distribution of migratory and resident fish species. In this case, the fish populations did not respond to the connectivity restoration immediately. It took 3–4 years for a clear response to occur, likely linked to a combination of increased connectivity and habitat change, and it is unclear whether a new equilibrium has been reached. European eel densities remain low and Atlantic salmon are absent, indicating that full recovery is still some way off.

5. Conclusions

This study suggests that subcatchment-scale connectivity restoration works have helped return the River Deerness to a more natural pre-impoundment species composition. The expected increases in rheophilic specialist species took several years to occur, so subcatchment-scale connectivity restoration projects need to set realistic timescales for achieving milestones in ecological community change. This should be paralleled, where possible, by consistent, high-quality monitoring incorporating Before-After and Control-Impact elements. This study also revealed that barrier removal is more effective in increasing the abundance of most native rheophilic fish species, and facilitating movement of poorly dispersing species, compared with fish pass construction. We recommend that all barriers, including those that are small, should be considered in catchment-scale restoration plans, and managers should aim for removal of all redundant barriers rather than installing fish passes, unless the risk of invasive species spread upstream is high. These findings have important implications for in-stream barrier management and river restoration works across the world. Given the paucity of existing studies in the literature, we encourage well-controlled long-term studies reporting the outcomes of large-scale connectivity restoration, particularly under differing environmental conditions and native faunas.

CRedit authorship contribution statement

Jingrui Sun: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Visualization, Writing – review & editing. **Jeroen S. Tummers:** Investigation, Writing – review & editing. **Shams M. Galib:** Investigation, Data curation, Writing – review & editing. **Martyn C. Lucas:** Conceptualization, Methodology, Investigation, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.149720>.

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